

A New *Photinus* Firefly, with Notes on Mating Behavior
and a Possible Case of Character Displacement
(Coleoptera: Lampyridae)

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The mating behavior of most Nearctic *Photinus* has been described (Lloyd, 1966a). Since that investigation a new species, a sibling of *Photinus pyralis* (Linnaeus), has been discovered and studied, and additional observations have been made on a photinid that was only briefly observed during the above study.

Methods, materials, and equipment used here were described in the report cited above.

Photinus concisus Lloyd, NEW SPECIES

BEHAVIOR: The deme studied was on an oak hillside in deep weeds and over the edge of an adjacent lawn in Kerrville, Texas. Observations were made between 31 May and 6 June, 1966.

Male flashing activity began between 18 and 27 minutes after sunset, continued at a high level for about 20 minutes and then slowly diminished. By one hour after sunset only an occasional flashing male was seen.

Males usually fly about one meter above the ground and during each flash (flash pattern = single flash) fly in a short arc. Arcs are usually in the horizontal plane, but upward or downward arcs (vertical plane) are sometimes executed. During each flash 10-20 cm. are traversed and between flashes 30-100 cm. Late in the activity period males generally fly 2-4 meters above the ground, and cover much longer distances during and between flashes. Flashes of several males were compared to flashes of an electronic flasher and appeared to be 0.3-0.4 seconds in duration at 74°F. Flash pattern interval varied slightly with temperature (72°, range 1.9-3.0, $\bar{x} = 2.3$, $n = 16$; 76°, range 1.7-2.4, $\bar{x} = 2.1$, $n = 6$).

Females were found on vegetation within one meter of the ground. They responded to the flashes of males and the flashlight with single-pulsed flashes at short delays. The flashes of one recorded female averaged 0.58 seconds in duration and were emitted at an average delay time of 0.57 seconds at 73° (Tables 1 and 2). Male approaches to females were observed; two to five flash exchanges took place during approaches.

A deme of *pyralis* in the same site was also observed. This species began activity 15-20 minutes earlier than *concisus* and its peak activity ended a few minutes after *concisus* began. Female delay time in *pyralis* has been previously reported for individuals collected in eastern United States (McDermott, 1911; Buck, 1937;

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Lloyd, 1966a). Females from Kerrville behave similarly. Three were timed with a stopwatch and their delays at 73° were 2.0, 2.1, and 2.3 seconds. Eight were recorded electronically (Tables 1 and 2).

TABLE 1

Species	Locality	Female No.	Temp. (F°)	Mean (Sec)	Range (Sec)	s.d.	n
<i>concisus</i>	Kerrville	1	73	0.57	.48-.62	.036	23
"	"	2	73	0.50	.48-.54	.020	11
"	"	4	73	0.67	.63-.70	.030	5
"	"	3	73	0.57	.51-.62	.032	10
"	"	5	73	0.55	.48-.63	.035	18
<i>pyralis</i>	"	1	76	2.08	2.05-2.12	.035	3
"	"	2	76	2.11	2.05-2.21	.062	6
"	"	3	76	2.02	1.90-2.11	.108	3
"	"	4	76	2.25	2.10-2.45	.110	9
"	"	5	76	2.16	2.03-2.23	.069	7
"	"	6	76	2.28	2.28-2.28	—	2
"	"	7	76	2.23	2.04-2.41	.121	10
"	"	8	76	2.12	2.05-2.22	.091	3
<i>dimissus</i>	Jarrell	1	76	0.17	.14-.21	.014	55
"	"	2	76	0.23	.22-.24	.010	3
"	"	3	76	0.20	.17-.22	.014	12

TABLE 1. Female Delays. Delays are timed from the start of stimulus flashes to the start of response-flashes. Artificial flashes used to stimulate females were similar in duration to flashes produced by males.

Because the male flash lengths of *pyralis* and *concisus* are similar, if not identical, and there is time and space overlap in their activity, captive females of both species were closely observed to determine whether or not cross-specific signalling occurs. Nine *pyralis* females in glass cages were arranged in an arc at 0.5 meter intervals. They flashed in response to the flashes of both *pyralis* and *concisus* males but attracted only *pyralis* males. *Concisus* males either continued in the direction they had been traveling, turned and flashed again and then flew off, or turned and flashed several times before flying away. Seven *concisus* females were tested in a similar fashion. They responded to flash patterns of males of both species and attracted several *concisus* males, but no *pyralis* males. One *concisus* female was placed in an arc with five *pyralis* females. All females responded to *concisus* males, and within a period of five minutes two were attracted to the *concisus* female. None were attracted to the *pyralis* females. This last test was conducted late in the evening, and no *pyralis* males flashed over the females.

It is unquestionably the female time delay that keeps males from coming into physical contact with sibling (i.e. heterospecific) females. Although there is a difference in the activity time of males of the two species, females of *pyralis* continue to flash-respond long after most of their males have ended their activity and

TABLE 2

Species	Locality	Female No.	Temp. (F°)	Mean (Sec)	Range (Sec)	s.d.	n
<i>concisus</i>	Kerrville	1	73	0.58	.28-.76	.124	23
"	"	2	73	0.50	.39-.56	.051	11
"	"	3	73	0.84	.60-.96	.134	10
"	"	4	73	0.67	.20-.72	.207	5
"	"	5	73	0.47	.24-.64	.103	18
<i>pyralis</i>	"	1	76	0.34	.32-.36	.020	3
"	"	2	76	0.34	.29-.38	.033	6
"	"	3	76	0.39	.35-.41	.032	3
"	"	4	76	0.30	.25-.45	.061	9
"	"	5	76	0.46	.36-.51	.055	7
"	"	6	76	0.44	.39-.48	—	2
"	"	7	76	0.36	.22-.54	.096	10
"	"	8	76	0.45	.42-.48	.030	3
<i>dimissus</i>	Jarrell	1	76	0.38	.08-.84	.191	55
"	"	2	76	0.29	.20-.36	.081	3
"	"	3	76	0.47	.28-.78	.145	12

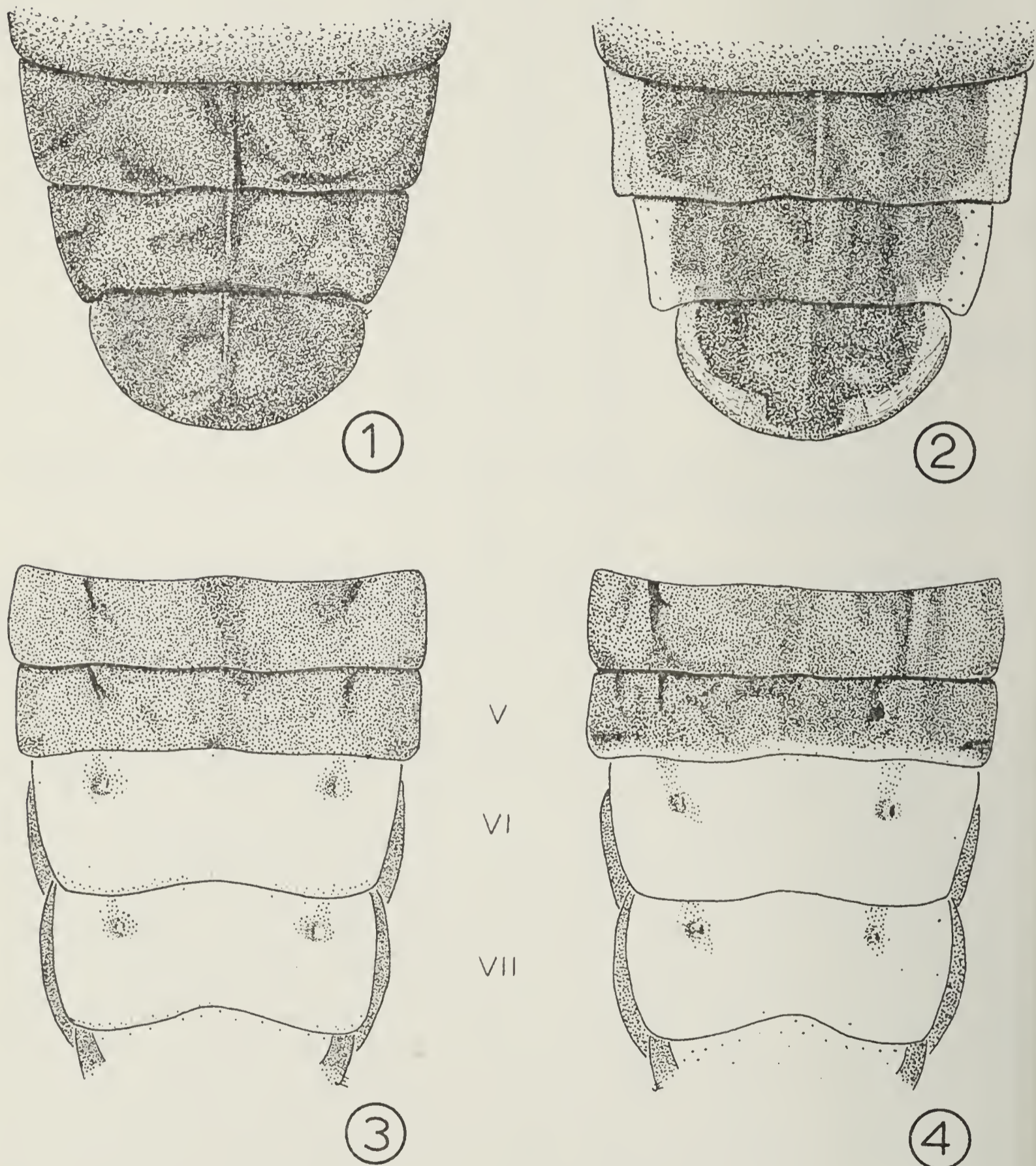
TABLE 2. Female Flash Lengths. Artificial flashes used to stimulate females were similar in duration to flashes produced by males.

they do answer *concisus* males. On the other hand, *concisus* females never answer flashlight flashes or *pyralis* males during the first 20 minutes of *pyralis* activity.

DIAGNOSIS: *P. concisus* has previously been confused with *Photinus pyralis* (Linnaeus). Male flash pattern emitted about every two seconds (versus about every six seconds in *pyralis*). Female response-delay about 0.6 seconds in duration (versus about 2.2 seconds in *pyralis*). Antepenultimate tergite entirely black (Figure 1) (versus with translucent (usually appearing white, cream, or pink) lateral edges in *pyralis*) (Figure 2). Ratio of total width of pronotal lateral margins (flanges to pronotal width greater than 0.31 (versus less than 0.31 in *pyralis*) (see below regarding geographic variation of this character). Lateral explanate margin of pronotum flat (versus with a ridge immediately mesal the submarginal row of punctures in *pyralis*)². Entire surface of ventral segment 5 entirely black or brown (Figure 3) (versus with a variable translucent-yellow apical margin in *pyralis*) (Figure 4). Pits on pronotal lateral explanate margin numerous and closely spaced (versus pits relatively sparse in *pyralis*). Less constant characters are 1) the coloration of the penultimate tergite, usually completely dark in *concisus* and with translucent (appearing white) lateral borders in *pyralis*, 2) the coloration of the pygidium, usually with fuscous-translucent areas in *concisus* and with translucent or yellow-translucent areas in *pyralis*, 3) the pink coloration of the hypomera usually confined to the hypomera in *concisus* and extending irregu-

²This ridge is most obvious if the specimen is viewed dorsally with rays from a microscope lamp passing across the pronotum at a low angle.

larly upon the pronotal flange in *pyralis*, and 4) the coloration of the mesepimera, black in *concisus* and fuscous-or black-orange in *pyralis*. *P. concisus* vouchers are, on the average, 0.7 mm. (male) and 0.8 mm. (female) shorter than their Kerrville *pyralis* voucher counterparts.



FIGURES 1-4. 1. Abdominal tergites *P. concisus* n. sp. 2. Abdominal tergites *P. pyralis* (Linnaeus). This character is the most consistent morphological character. The figure shows the usual condition. The slightest indication of a translucent area at the lateral edge of the antepenultimate tergite will identify the specimen as *pyralis* (male only). 3. Ventral abdominal segments *P. concisus* n. sp. 4. Ventral abdominal segments *P. pyralis* (Linnaeus). Pale margin variable, sometimes lacking.

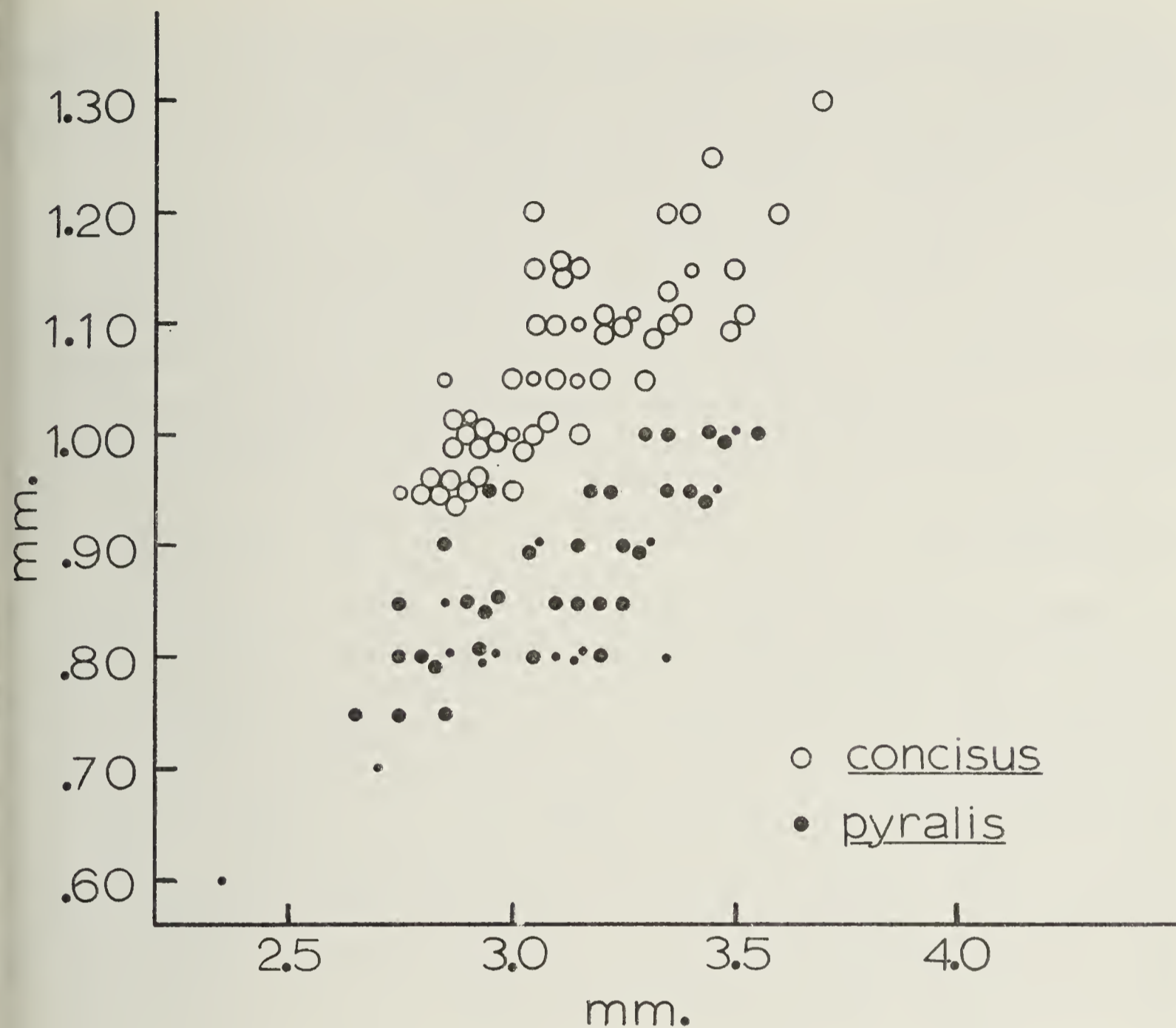


FIGURE 5. Pronotal proportions of behavior voucher specimens of *pyralis* and *concisus* from Kerrville, Texas. Small symbols indicate females. Horizontal axis=pronotal width, vertical axis=combined width of pronotal lateral explanate margins. Note the nearly complete separation.

HOLOTYPE: Male. Form as in *pyralis* (see Green, 1956). Length 11.5 mm. Eyes large, separated above by less than diameter of eye. Pronotum without central dark spot; with central, rectangular, glossy rufous spot; with numerous closely spaced pits (excluding central raised disk); with total width of pronotal lateral explanate margins 0.36 width of pronotum; with pink pigment of hypomera only slightly and irregularly extending upon ventral surface of pronotal explanate margin. Scutellum and mesonotal areas fuscous and rufous, respectively. Elytra black; sutural bead yellow; lateral explanate margin yellow, becoming fuscous and black apically. Mesepimera black. Ventral abdominal segments 2-5 entirely black, 6 and 7 yellow and luminous, 8 yellow with translucent areas, 9 fuscous. Dorsal surface of penultimate and antepenultimate segments entirely black. Pygidium rounded, brown with small fuscous-translucent area each side. Aedeagus as in *pyralis* (see Green). Flash pattern a single flash about 0.4 seconds in duration; emitted about every two seconds of flight.

TYPE LOCALITY: Texas: Kerr County, 1 mile NE Kerrville on Route 16. 1 June, 1966. J. E. Lloyd. Dry hillside over weeds and adjacent lawn in oak grove. Lloyd No. 6679; one of thirteen specimens collected singly by hand on the above date after flash pattern interval was timed with a stopwatch. Deposited in the collection at Cornell University: C. U. Type No. 4411.

VARIATION: Length 9.3-12.5 mm. Four specimens have a fuscous central pronotal spot. See Figures 5 and 7 for variation in pronotal proportions. Ventral surface of pronotal explanate margin usually without pink pigment; pigment usually confined to hypomera. Scutellum fuscous or yellow. Yellow elytral border nearly absent in some specimens and covers only the bead; in others it is wider than explanate margin. Sutural bead fuscous or with narrow yellow line. Pygidium entirely black, with black "T" surrounded by fuscous translucent cuticle, or with a fuscous-translucent margin. Penultimate segment dorsally occasionally with lateral fuscous areas.

FEMALES: Length 8.9-10.7 mm. Alate, similar to males in form and coloration. Eyes small, separated above by more than diameter of eye. Pronotal and elytral coloration as in males although sometimes sutural bead and explanate margin completely black. Pronotal proportions as indicated in Figure 5. Pygidium entirely yellow or with fuscous basal spot. Ventral abdominal segment 6 with central, glossy yellow, reniform light organ and remainder of surface black, or with yellow (luminous tissue?) or pale apical margin. Female flash-response a single flash about 0.6 seconds in duration and emitted approximately 0.6 seconds after beginning of male flash. *Concisus* females have pronotal ratios exceeding 0.31 (versus ratios less than 0.31 in *pyralis* females; see below). They also have flat pronotal flanges (versus with submarginal ridges in *pyralis*).

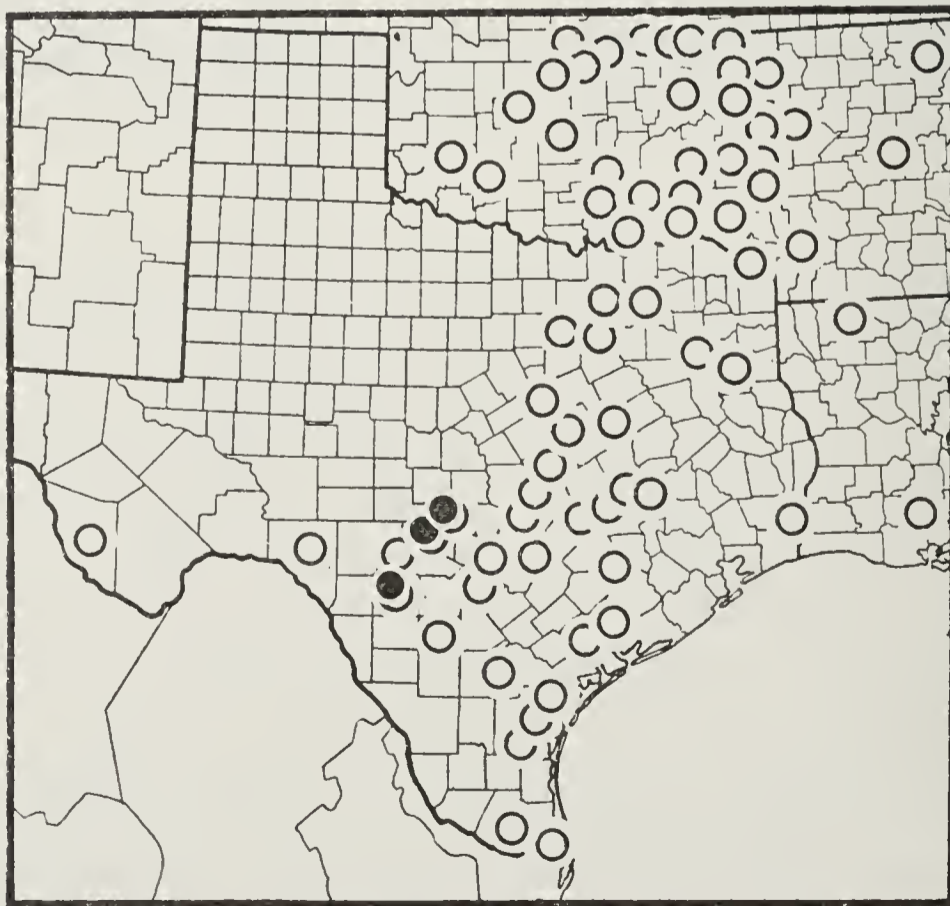


FIGURE 6. Distribution of *P. concisus* n. sp. in dots and that *P. pyralis* (L.) in circles. *Pyralis* occurs throughout the eastern U. S. (Lloyd, 1966a map).

DISTRIBUTION: See Figure 6. Nearly 400 specimens from Kansas, Arkansas, Oklahoma, and Texas, previously identified as *pyralis*, were reviewed to determine the distribution of *concisus*. TEXAS (no locality). Belfrage, two males (MCZ)³. TEXAS. Uvalde Co., Garner St. Pk., 32 mi. N. Uvalde (Frio Riv.) \pm 1800 ft., 15 Aug. 1955, T. J. Cohn, one female (UMMZ). TEXAS. Uvalde Co., V-20-38, J. H. Robinson, one male (CAS). TEXAS. Gillispie Co., VI-23-40, D. J. and S. N. Knull, two males, two females (OSU). Behavior vouchers collected at type locality (see above) Holotype, 44 males, 9 females.

NOTES: This species is named for the short flash pattern interval and short female delay as compared with its close relative, *P. pyralis*.

P. pyralis behavior vouchers collected at the *concisus* type locality, 33 males, 14 females.

The morphological characters given to distinguish *concisus* from *pyralis* permit correct identification of all voucher specimens of both species.

Green (1956), in his revision of *Photinus*, noted variations in *pyralis* from Brownsville, Texas, and one specimen from Uvalde. I have seen these; the Uvalde specimen is *concisus* (see above, Coll. Robinson) and I will defer judgement on the identity of the Brownsville specimens until I have made field observations.

LeConte (1881) described *Photinus benignus*. In his collection (Museum of Comparative Zoology) are a male and female labeled *benignus*; Dallas, Texas, Boll. The male bears a red label: Type 2792. The female is numbered "2." LeConte did not designate a holotype nor has anyone since, a lectotype. I have labeled the male "Lectotype, *Photinus benignus* LeConte: Lloyd, J. 1966," and the female "Lectallotype *Photinus benignus* LeConte: Lloyd, J. 1966." Both of these specimens are *P. pyralis*. Green (1956) correctly synonymized *benignus*.

The following change in Green's key is made: Couplet 9, page 566, should read:

- | | | |
|---|------------------------------|----|
| 9. Ventral segments 6 and 7 transversely convex; segment 5 with pale apical border (except in <i>P. concisus</i> which occurs in central Texas only)..... | <i>P. pyralis</i> group..... | 12 |
| Ventral segments 6 and 7 nearly flat; segment 5 entirely dark piceous or black | | 10 |

The following addition to Green's key is made: Couplet 13, page 566:

- | | | |
|---|-------------------------------|-----|
| 13. Mandibles slender, etc..... | <i>P. australis</i> Green. | |
| Mandibles stout. Head nearly flat between eyes, surface smooth, with simple punctulation. Ventral segments 2 to 4 entirely dark piceous. Size larger, form more elongate..... | | 13A |
| 13A. Antepenultimate tergite entirely black; ventral segment 5 entirely black..... | <i>P. concisus</i> Lloyd. | |
| Antepenultimate tergite with translucent or white lateral borders; ventral segment 5 with pale apical margin..... | <i>P. pyralis</i> (Linnaeus). | |

³Belfrage was a mid-nineteenth century collector who collected extensively in the Waco-Clifton region of Texas, as well as near San Antonio and Austin. In 1870 he made a two month collecting trip into West Texas. A collection of insects from Waco which he sold to Dr. H. A. Hagen was later presented to the Museum of Comparative Zoology, Harvard College (Geiser, 1937).

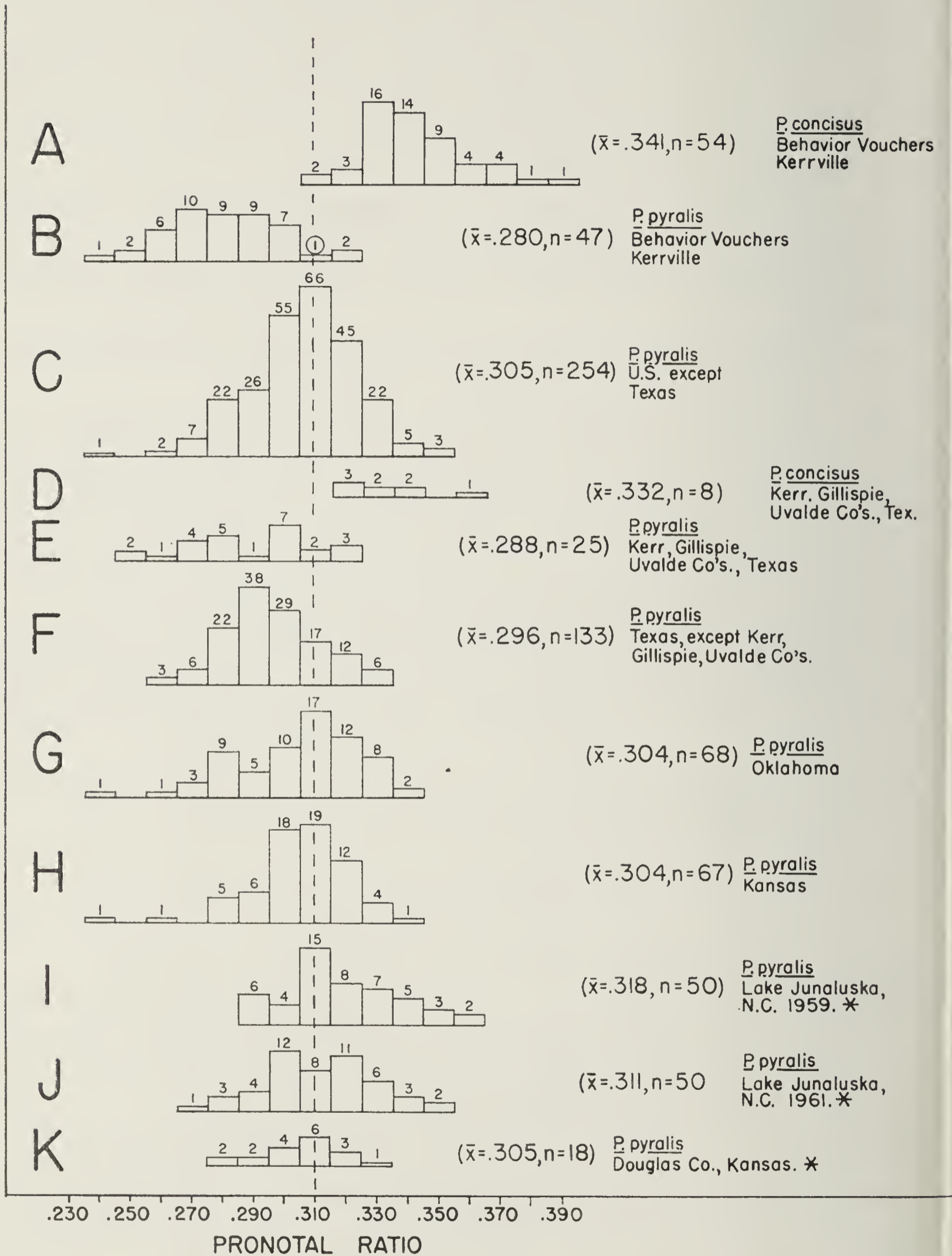


FIGURE 7. Pronotal ratios for *concisus* and *pyralis* from various localities as indicated. D includes the two Belfrage specimens of unknown origin. *L. Junaluska, North Carolina, 29 June, 1959 and 28 June, 1961, H. V. Weems; Douglas County, Kansas, June 28, 1919, W. E. Hoffman.

GEOGRAPHIC VARIATION OF PRONOTAL
PROPORTIONS—CHARACTER DISPLACEMENT?

There is nearly complete separation of Kerrville *concisus* and *pyralis* when the width of the pronotal explanate margins (flanges) is plotted as a function of total pronotal width (Figures 5 and 7 A, B). A similar separation is found if marginal width is plotted as a function of body length. No separation occurs when the width of the pronotal central disk is plotted against body length.

Pronotal proportions for *pyralis* specimens from outside Kerr, Gillispie and Uvalde Counties (i.e. Texas, other counties, and Oklahoma, Kansas, Arkansas, Illinois, Ohio, etc.) are variable and fall within, as well as on both sides of, the hiatus that largely separates voucher *pyralis* and *concisus* (Figure 7 C). Two possible explanations for the separation of these values (i.e. the cut-off of high *pyralis* values) are: 1) Pronotal proportion values are grouped in inbred demes and the demes I sampled at Kerrville "happened" to be nearly mutually exclusive. The data do not suggest this; a) museum specimens of *concisus* and *pyralis* from Kerr, Gillispie, and Uvalde Counties also show this separation (Figure 7 D, E), and b) there is broad variation in pronotal ratios in series of museum specimens that apparently were taken from single demes elsewhere (Figure 7 I, J, K). 2) The pronotal ratio in *pyralis* is correlated (e.g., pleiotropy) with some aspect of the beetle's ecology and in the Edwards Plateau portion of its range ecological conditions limit certain variation that is tolerated in other localities. Figure 7 shows the distribution of *pyralis* ratios for various localities. The means are similar for "all U. S. except Texas" (Figure 7 C), for Kansas only (Figure 7 H), and for Oklahoma only (Figure 7 G). The mean for Texas specimens from counties *other than* Kerr, Gillispie, and Uvalde is lower (Figure 7 F), and the mean for Kerr, Gillispie and Uvalde *pyralis* is lowest (Figure 7 E).

One element in the environment of *pyralis* that is different in the Edwards Plateau portion of its range is the presence of *concisus* and this may be a case of character displacement (Brown and Wilson, 1956), but the width of the pronotal margins is certainly only indirectly involved (Mayr, 1963 (p. 311)).

Photinus dimissus LeConte

This species occurs in Texas and southern Oklahoma (see map, Lloyd, 1966a) and is found in meadows, pastures, and fields. Observations were made near Jarrell, Williamson County, Texas, 27-29 May, on a population that numbered hundreds of individuals.

Male flashing activity began between 17 and 26 minutes after sunset and ended except for a few stragglers by 2 hours after sunset. Males fly within two meters of the ground, usually just above the tips of vegetation in straight or meandering flight. The male flash pattern is a single flash about 0.2 seconds in duration at temperatures near 70°. Flash pattern interval is about one second in duration (67-68°, range 0.7-1.7, $\bar{x} = 1.0$, $n = 22$). Males fly 5-10 cm. during the flash and 20-100 cm. between flashes. Their light-trails are variable in form: straight, curved, or hooked, and with rises or dips.

Females were found on the ground. They responded to flashes of males and the flashlight with single-pulsed flashes at short delays. The flashes of one recorded female averaged 0.38 seconds in duration and were emitted at an average delay time of 0.17 seconds at 76° (Figures 1 and 2). This is the shortest delay yet recorded for any firefly (Lloyd, 1966a, b).

Male approaches to captive and free females were observed. Several exchanges of signals were usually required for a complete approach. Females didn't answer every male flash (although the morpheme is the single flash) and sometimes would fail to answer as many as six consecutive flashes. Male flash intervals during the approaches were more variable than those in advertising males.

On one occasion I noticed that two flashes of a male on the ground followed immediately those of a flying male. The flying male turned and approached, but then hesitated and eventually flew away after the flashes of the grounded male began to precede his own.

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LITERATURE CITED

- BUCK, J. B., 1937. Studies on the firefly II. The signal system and color vision in *Photinus pyralis*. *Physiol. Zool.* 10:412-419.
- GEISER, S. W., 1937. Naturalists of the frontier. Published by the author.
- GREEN, J. W., 1956. Revision of the Nearctic species of *Photinus* (Lampyridae: Coleoptera). *Proc. Calif. Acad. Sci.* 28(15):561-613, 19 figures.
- LECONTE, J. L., 1881. Synopsis of the Lampyridae of the United States. *American Ent. Soc., Trans.* 9:15-72.
- LLOYD, J. E., 1966a. Studies on the flash communication system in *Photinus* fireflies. *Univ. Mich. Mus. Zool., Misc. Pub. no. 130*, pp. 95.
- LLOYD, J. E., 1966b. Signals and mating behavior in several fireflies (Coleoptera: Lampyridae). *Col. Bull.* 20:84-90.
- MAYR, E., 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Mass.; 797 pp.
- MCDERMOTT, F. A., 1911. Some further observations on the light-emission of American Lampyridae: the photogenic function as a mating adaption in the Photinini. 43:399-406.
- MCDERMOTT, F. A., 1966. Coleopterorum Catalogus Supplementa, Pars 9, (Editio Secunda) Lampyridae. pp. 149. (Ed. W. O. Steel) W. Junk, Gravenhage.